The Effects of Spatial Constraints on Fish Shoal Cohesion

STUART D. FITZSIMMONS AND KEVIN WARBURTON
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Department of Zoology, University of Queensland, St. Lucia, Queensland 4072

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Using shoals of four individuals, the effects of different experimental treatments on the movement behaviour and group cohesion of mullet were examined. Mean swimming speeds significantly increased with the presence of a patch of weed, whilst mean turning frequencies significantly increased as tank size decreased. Mean interfish distances and separation angles did not vary significantly between different treatments.

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INTRODUCTION

Although many aspects of fish schooling and shoaling behaviour have been previously investigated through controlled laboratory experiments (see review by Pitcher and Parrish 1993), there is limited information available concerning the effects of housing conditions on shoaling behaviour. The aim of the present study was to examine the effects of tank size and structural complexity (the presence or absence of vegetation), on the swimming behaviour of individuals and overall group cohesion. Kleerekoper et al. (1970) reported that as tank size decreased, swimming speeds of individuals decreased and turning rates increased. Tank size has also been shown by other workers to affect swimming speed and group polarity (Inagaki et al. 1976, Sakamoto et al. 1976, Aoki 1980). Andorfer (1980) found that structural complexity, in the form of a centrally located cylinder, had a concentrating effect on groups. However, no study to date has examined the behaviour of identified group members. This study differed from previous studies by concentrating on known focal individuals within groups over a range of different treatments.

MATERIALS AND METHODS

Juvenile mullet, *Mugil cephalus*, (mean fork lengths 68 to 82mm) were caught by seine net in a freshwater creek at Karana Downs, southeast Queensland. Fish were transported to the laboratory and placed in filtered aquaria. A total of 24 fish were used in a six block experiment conducted over a period of 14 days. Each block consisted of a shoal of four individuals, which were subjected to three treatments: control tank (110 x 110 x 30cm), reduced tank (55 x 55 x 30cm), and structured tank (110 x 110 x 30cm with a centrally located 30 x 30 x 10cm patch of artificial weed). The tanks were filled to a depth of 15cm. The order of the trials was randomised, with no shoal being subjected to more than one trial per day. All individuals remained identifiable by slight differences in size and body patterns. Home tanks housed four fish (all from a given block) between trials. Trials were carried out between 1000 and 1400h under conditions of natural light, water temperature remained constant at 22 ± 2°C. The bottom of both tanks was opaque white to provide maximum contrast for video analysis. At the beginning of each trial, fish were removed from the home tank, placed in the test tank, and left undisturbed for 50 minutes prior to video recording. Each group was filmed for 10 minutes using a National Panasonic video camera suspended above the centre of the tank. A sequence of 100 frames (1 frame = 1 sec) was chosen at random from a 10 minute recording. A Dapple II-GS Image Analyser was used to digitise the co-ordinates of each fish's head and tail. A BASIC program was used to calculate mean swimming speeds (body lengths s^{-1}), mean direction of movement (degrees) from headings of individual fish using circular statistics, and mean interfish distances (body lengths). Separation angle (degrees) was calculated from mean direction of movement, and represented a measurement of the polarisation of individuals within the group. Mean turning frequencies were obtained from plots of swimming trails, and log-transformed prior to analysis to stabilise the variance. A two-way ANOVA with Tukey's multiple range test was used to analyse significant differences between treatments. All analyses were performed using generalised linear procedures (SAS Institute 1986).

RESULTS

Tank size and the presence of 3-D structure had a significant effect on mean swimming speeds and turning frequencies ($F = 8.59$, $p < 0.005$; $F = 239.12$, $p < 0.0001$ respectively). Multiple range testing indicated that mean swimming speeds were significantly higher when a structure was present. Mean swimming speeds did not differ significantly between groups in the reduced tank and control treatments (Fig. 1). Mean turning frequencies were significantly higher in the reduced tank compared to the control and structured treatments (by factors of 2.6 times and 2.0 times respectively).

Mean interfish distances and separation angles did not vary significantly between treatments according to the two-way ANOVA ($p > 0.05$) (Fig. 1). Separation angle, a measure of the polarisation of the individuals within the group, was highest in the smaller tank and lowest in the structured tank. Individuals within each treatment maintained an interfish distance of approximately 0.95 body lengths.

DISCUSSION

Previous studies have recorded the schooling and shoaling behaviour of fish within tanks without taking into consideration tank size or structure. This study found that swimming speeds and turning frequencies were significantly influenced by both tank size and structural complexity. Swimming speeds decreased and turning frequencies increased with a reduction in tank size. Individuals in the smaller tank performed slow moving circles covering only short distances, which may have been due to the limited swimming area available to the fish, as observed by Kleerekoper et al. (1970).

Fish within the smaller tank performed more turns compared to those in the control and structured tanks, probably because they had a higher chance of encountering the walls of the tank. Inagaki et al. (1976), suggested that the polarity of fish in schools would be affected by tank size, due to fish depolarising when they encountered a wall, and then repolarising as they moved away. Results obtained in this study suggested that tank size and the presence of a structure had a definite, although not statistically significant, effect on the behaviour of individuals, as well as on the abilities of the individuals to co-ordinate their movements in a cohesive manner. Tank size and structural complexity should be considered when analysing interactive fish behaviour so that analysis of movement behaviour (swimming speeds and turning frequencies) and group cohesion (interfish distances and separation angles) is not biased by these conditions.

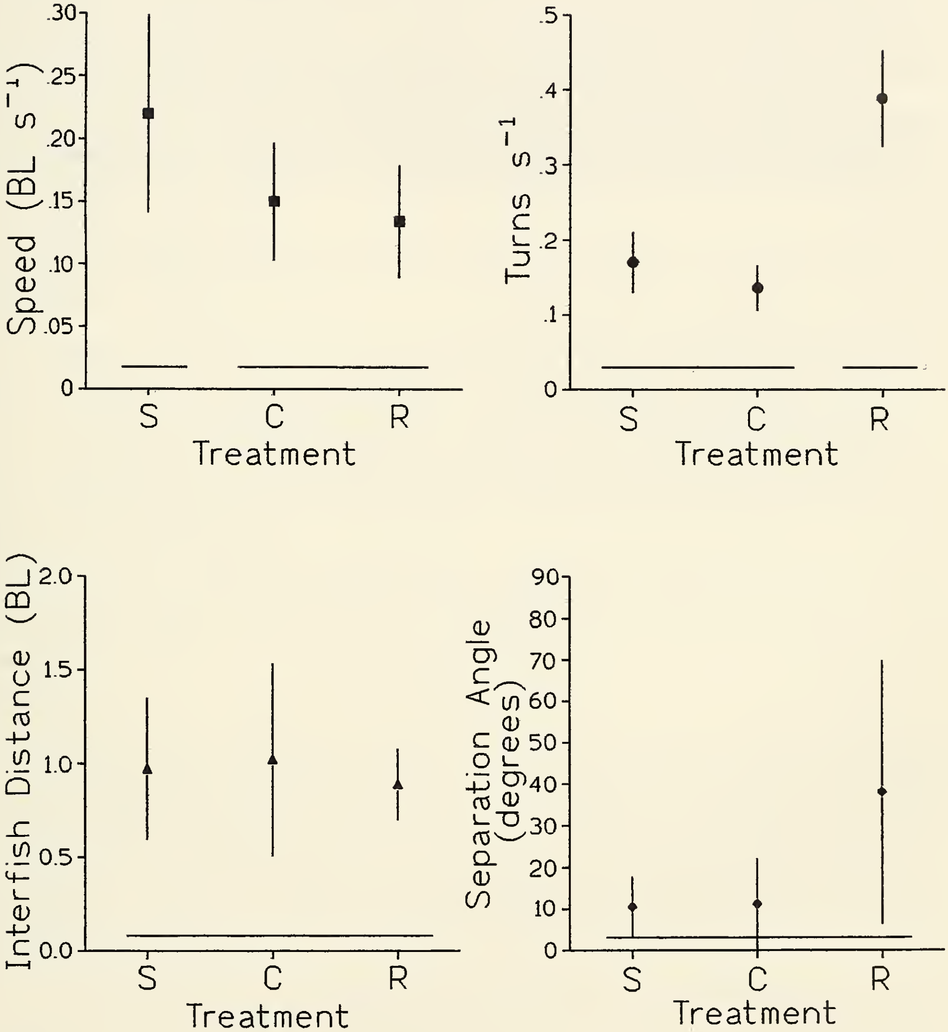

Fig. 1. The effects of treatment on mean swimming speed (body length s^{-1}), mean turning frequency (turns s^{-1}), interfish distance (BL) and separation angle (degrees). S = Structured Tank, C = Control Tank, R = Reduced Tank. Filled symbols and vertical lines indicate means and standard errors for pairs of fish, and horizontal lines connect treatments which did not differ significantly at the 5% level according to the two-way ANOVA.

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